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Higher alpha and gamma, but not beta diversity in tropical than in Mediterranean temporary ponds: A multi-taxon spatiotemporal approach

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Abstract

The latitudinal diversity gradient predicts that tropical regions should have higher alpha, beta, and gamma diversity than temperate areas. However, only a few studies have assessed the temporal variability of the different components of diversity across climatic regions. In this study, we compare, using a spatial and temporal approach, the diversity of multiple taxa inhabiting tropical and Mediterranean temporary ponds. We sampled the biological communities of each set of ponds on three occasions during the same hydrological year. Under a spatial framework, we analyzed, alpha, beta, and gamma diversities. With a temporal approach, we compared the coefficients of variation in alpha diversity for each local community, and temporal beta diversity. Differences between regions and sampling periods were tested using generalized linear mixed models. We found higher gamma and alpha diversity in the tropical ponds, as expected given the latitudinal differences between them. However, phytoplankton and microinvertebrates from the Mediterranean region, matched or even exceeded tropical alpha diversity on some occasions. Spatial beta diversity did not differ between regions, and it showed lower values at the middle or the end of the hydroperiod in bacteria, micro- and macroinvertebrates and amphibians. Thus, processes homogenizing and heterogenising pond metacommunities must be balanced in both studied regions. Temporal variation in alpha and beta diversity was similar for ponds in both regions, except for macroinvertebrates and amphibians, suggesting differential effects on community variation observable only in animals with longer life-spans, at our temporal scale of analysis.

The search for global ecological patterns is one of the main aims of macroecology and biogeography. From gradients in body size and body proportions (Bergmann 1847; Allen 1876) to distribution ranges (Rapoport 1975), patterns across biogeographic regions have always been of major interest for ecologists. The latitudinal diversity gradient is perhaps the best described pattern (Rosenzweig 1995; Hillebrand 2004). This biogeographic "rule" establishes that biodiversity is

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negatively correlated with latitude, with tropical regions holding higher diversity than temperate ones. A varied array of factors have been suggested as responsible for the higher biodiversity in the tropics: larger geographical area (Terborgh 1973), more overlapped distribution ranges due to mid-domain effects (Colwell and Lees 2000), higher productivity (Pianka 1966), lower environmental severity (Francis and Currie 2003), lower environmental unpredictability and higher seasonal and historical stability (e.g., less affected by glaciations; Brown and Lomolino 1998; Gaston and Blackburn 2000), higher evolutionary rates (Rohde 1992; "the Red Queen runs faster when she is hot", Brown 2014), or higher coexistence facilitated by complex biotic interactions (Roslin et al. 2017). Nevertheless, most empirical studies compare only a few taxa (mostly terrestrial vertebrates or plants) across the latitudinal gradient, and those that compare several groups of organisms estimate diversity from an heterogeneous set of published sources (i.e., Currie 1991).

Biological diversity is composed of three components: alpha, beta, and gamma (Whittaker 1972). Classically, gamma diversity has been considered higher in the tropics, as most macroecology studies show when comparing regional diversities across the globe (e.g., Hillebrand 2004). But high gamma diversity can be the result of high alpha diversity (more diverse local patches) and/or high beta diversity (more dissimilar local patches). There is a broad consensus that there is higher alpha diversity in the tropics (e.g., France 1992; Rex et al. 2000; Qian and Song 2013) and many investigations find a strong positive correlation between alpha and gamma diversities (Arellano and Halffter 2003; García et al. 2007). Many studies have also found spatial beta diversity to be higher in regions at lower latitudes (Cao et al. 2021; Muñoz-Mazón et al. 2021). To explain these larger dissimilarities among sites (i.e., higher spatial beta diversity) in the tropics, many authors have hypothesized that more geographically patterned environment (Rosenzweig 1995), higher speciation rates (Rohde 1992), smaller distribution ranges (Stevens 1989) or stronger dispersal barriers (mountains are "higher" in the tropics; Janzen 1967) lead to more endemicity in the tropics and, lastly, to higher species replacement and hence beta diversity (Qian and Xiao 2012). In contrast, environmental heterogeneity, which is expected to be lower in the tropics, is known to be positively related with beta diversity (Stein et al. 2014; Fernández-Aláez et al. 2020). Tropical ecosystems can be heterogeneous at small scales but relatively homogeneous at larger scales, in contrast to higher latitudes, where the environment shows high variability in space and time (Soininen et al. 2007; Graco-Roza et al. 2022).

Large-scale empirical studies comparing biological diversity between biogeographic regions are usually addressed from a spatial focus, in the sense that they compare multiple sites without considering temporal dynamics (e.g., Myers et al. 2013). When time is considered, an extended spatial approach is often used, comparing snapshot data from multiple sites over time. In other words, multiple patches are simultaneously compared to each other, and the same procedure is repeated at different times (e.g., Soares et al. 2015). However, a purely temporal approach, comparing the variability in diversities of each single patch of a metacommunity across different times, in large spatial extents, has rarely been carried out (e.g., Liang et al. 2015; Nunes et al. 2020).

When comparing the biological diversity of freshwater ecosystems in distinct regions such as tropical and temperate climates, the particular characteristics of each climate must be considered. While temperate climates exhibit strong seasonality in terms of temperature, this is typically more constant in the tropics. In contrast, precipitation may widely vary through the year at lower latitudes, especially in tropical climates (MacArthur 1972; Fick and Hijmans 2017), although precipitation in the temperate Mediterranean climate can also be very variable (Blondel et al. 2010). Consequently, hydrology is an important driver of diversity and needs to be considered when comparing mostly isolated aquatic systems such as temporary ponds, irrespective of whether they are in the tropics or in temperate latitudes. Due to heavy precipitation in the rainy period of seasonal tropical climates, there may be a shift in the hydrological connectivity among close water bodies, with the flood pulse usually leading to environmental and metacommunity homogenization (Thomaz et al. 2007; Brasil et al. 2020). Despite hydrological differences between regions with different climates, temporary ponds suffer from natural cyclic disturbances (generally drying), community re-establishment and succession (Williams et al. 2007). Regardless of the biogeographic region, we can expect higher spatial beta diversity in early stages of the hydroperiod in some groups with resting forms, due to stochastic processes during egg bank hatching (Castillo-Escrivà et al. 2017). In contrast, as ecological succession proceeds through the hydroperiod, dispersal processes can homogenize communities within a region (Fodelianakis et al. 2019, Zeng et al. 2019).

In addition, lower variability and weaker seasonality are often argued to contribute to higher species richness in the tropics (Brown and Lomolino 1998; Gaston and Blackburn 2000). Temporal environmental heterogeneity is supposed to be lower in the tropics than in temperate regions (MacArthur 1972), at least in terms of temperatures. In the same way that high spatial environmental heterogeneity generates high alpha and spatial beta diversity (Stein et al. 2014; Fernández-Aláez et al. 2020), temporal environmental heterogeneity generates temporal variability in diversity (Alves-de-Souza et al. 2017). Thus, stronger temporal environmental heterogeneity in temperate regions than in the tropics could lead to higher temporal variability of biological diversity in these regions.

In this work, we quantify differences in alpha, beta and gamma diversity in freshwater ponds across two distant biogeographic regions located at different latitudes (Neotropical and Mediterranean). We use both a spatial approach across three sampling periods (to answer the question: which region

is more diverse?) and a temporal approach (to answer the question: which region's diversity is more variable?) (Fig. 1). To do so, we analyzed how the biological diversity of a wide range of aquatic taxa (from bacteria to amphibians) changes across space and time, using temporary ponds as model ecosystems. Our approach is based on Whittaker's framework of alpha, beta and gamma diversity. Specifically, we ask if tropical temporary ponds harbor higher biodiversity than Mediterranean temporary ponds, as expected due to latitudinal differences. Moreover, we aim to assess the contributions of both temporal and spatial alpha diversity, and temporal and spatial beta diversity to the observed patterns. For this purpose, we hypothesize that (1) gamma diversity will be higher in the tropical than in the Mediterranean ponds for all taxa; (2) higher gamma diversity in the tropical ponds will be supported by higher alpha and higher spatial beta diversity; (3) spatial beta diversity will decrease with the progression in the hydrological cycle in the tropical ponds, due to higher hydrological connectivity; and (4) Mediterranean ponds will show higher temporal beta diversity and alpha diversity variation than tropical ponds, due to higher temporal environmental heterogeneity.

Material and methods

Study area

We surveyed temporary ponds in two distant biogeographic regions: 23 tropical ponds in Costa Rica and 29 Mediterranean ponds in Spain (Fig. 2). These ponds were distributed in a similar spatial extent (10,000 km^2 in Northern Costa Rica and 13,000 km^2 in Eastern Spain) but with two distinct climates: tropical climate (almost constant warm temperatures and marked rainy and dry seasons) and Mediterranean climate (mild winter and warm summer, with lower precipitation, generally concentrated in spring and autumn; Köppen and Geiger 1936).

We selected natural or naturalized temporary freshwater ecosystems, with low human impact, from sea level up to 1500 m a.s.l., including farmland ponds, coastal wetlands, or inland shallow lakes. Despite hydroperiod ranging from at least 6 months to a few years (mostly temporary and fishless, but some semi-permanent and occasionally with fish), all these temporary ponds shared a shallow depth (always lower than 2 m) and mostly fresh to oligohaline salinity (generally < 3000 μS/cm). We visited each pond three times during the same hydrological year: once in the early hydroperiod, that is, about 2 weeks after the infilling of the ponds (May 2017 in Costa Rica, January 2018 in Spain); once again in the middle of the hydroperiod (October 2017 in Costa Rica, April 2018 in Spain); and one last time by the end of the hydroperiod of temporary ponds, before their drying (January 2018 in Costa Rica, June 2018 in Spain). We characterized the environment of each surveyed pond in each period as described in Gálvez et al. (2023) and Olmo et al. (2022). This environmental characterization included limnological variables, such as major ion and nutrient concentrations, water transparency, temperature, pH, conductivity, and oxygen concentration; biotic variables such as vegetation architecture, chlorophyll a concentration, livestock use and presence of fish; hydrogeomorphological variables such as depth, diameter, area, morphology, proportions of organic and carbonate content in the sediment, altitude above sea level,

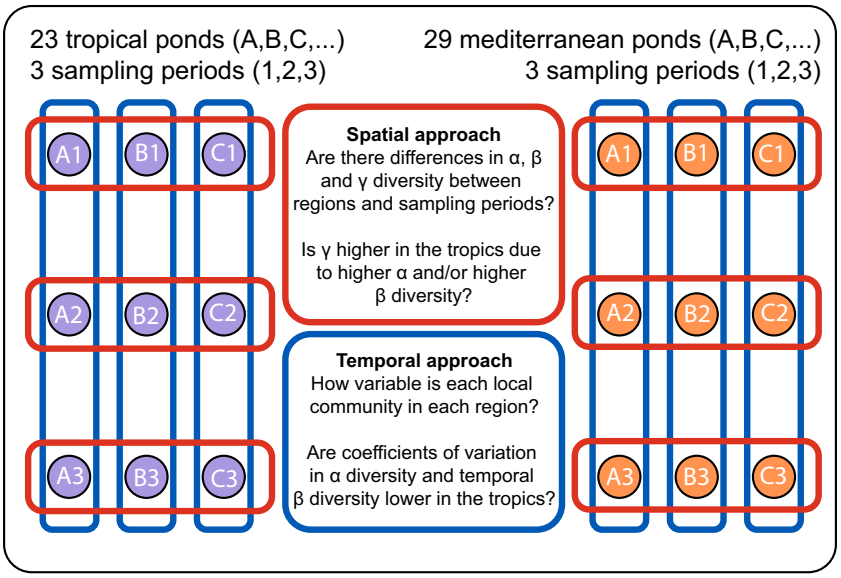

Fig. 1. Summary of the sampling design, aims and structure of the diversity analyses. Different measurements of biological diversity were obtained in order to test (i) for differences between regions and sampling periods and (ii) for differences between regions in the variability of each local patch. The same procedure was repeated for six different groups of organisms.

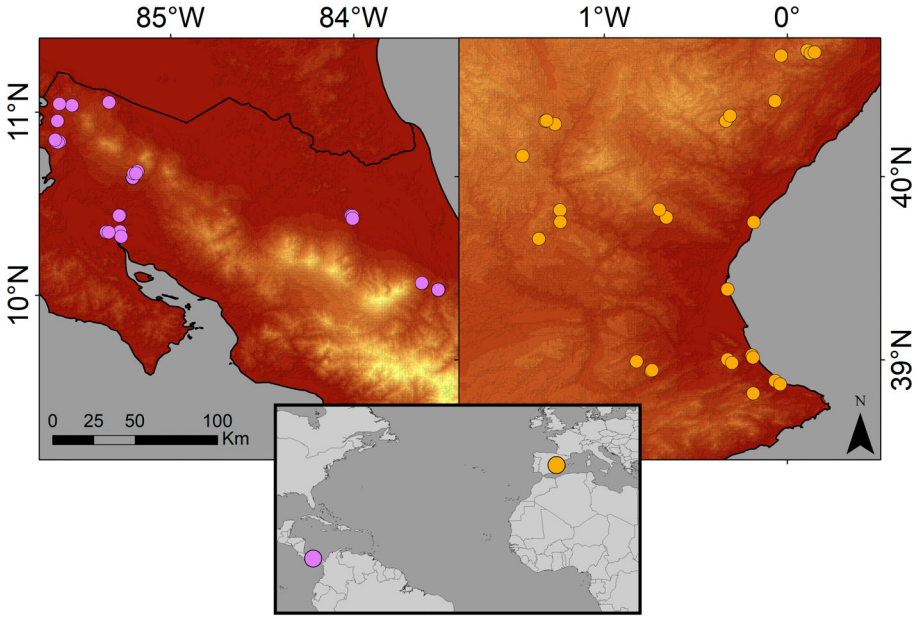

Fig. 2. Distribution of sampled temporary ponds in the study areas. Lilac dots represent tropical temporary ponds, located in Costa Rica, while orange dots represent Mediterranean temporary ponds, in Eastern Spain. Background colors represent altitude above sea level, from dark red (0 m a.s.l.) to bright yellow (3800 m a.s.l.).

hydroregime, origin of the water and granulometry of the sediment; landscape variables including proportions of land use type and landscape heterogeneity; and climatic variables.

Biological communities

In each of the three visits per pond in both regions, we characterized the biological communities of different groups of organisms, with the maximum taxonomic resolution possible, including bacteria, archaea, phytoplankton, microinvertebrates (rotifers, branchiopods, copepods, and ostracods), macroinvertebrates (mainly mollusks and insects, but also including scarcer groups such as bryozoans, annelids, flatworms, crayfish, etc.) and amphibians.

For next generation-targeted amplicon sequencing analysis of archaeal and bacterial communities, between 0.2 and 0.5 L of pond water were filtered in 0.2 μm pore polycarbonate filters (Nucleopore, Whatman™), after prefiltration of 1 L in 3 μm pore polycarbonate filters (Nucleopore, Whatman™). Samples were cold stored in microtubes filled with RNAlater™ reagent until further analysis. DNA extractions, PCR, and bioinformatics for taxonomic assignments were done following Picazo et al. (2019). Briefly, DNA extraction of 0.2 μm pore polycarbonate filters was performed with the EZNA™ Soil DNA isolation kit (Omega Bio-Tek, Norcross, GA, USA) following the instructions given by the supplier. After nanodrop quantification of each sample, sequencing of the region V4 of the 16S rRNA gene was done using the Illumina MiSeq system (2×250 bp) at the genomics facilities of the Research Technology Support Facility of Michigan State University, USA. For each sample, Illumina compatible, dual indexed amplicon libraries of the 16S-V4 rRNA hypervariable region were created with primers 515f/806r. PCR reactions were made following Kozich et al. 2013. Completed libraries were batch normalized using Invitrogen SequalPrep DNA normalization plates. Then, the Qubit quantified pool was loaded on a standard Illumina MiSeq v2 flow cell and sequencing was performed in a 2×250 bp paired end format using a MiSeq v2 500 cycle reagent cartridge. Custom sequencing and index primers complementary to the 515/806 target sequences were added to appropriate wells of reagent cartridge. Base calling was done by Illumina real time analysis (RTA) v1.18.54 and output of RTA was demultiplexed and converted to FastQ format with Illumina Bcl2fastq v2.19.1. Sequences were processed using the UPARSE pipeline using USEARCH v11.0.667 (Edgar 2013). After merging of read pairs, the dataset was filtered by a maximum number of expected errors of 0.5. Chimeric sequences were removed with USEARCH v11.0.667 utilizing the UCHIME (Edgar 2013), against the SILVA 138.1 database. Filtered sequences were clustered in zero-radius Operational Taxonomic Units (ZOTUs), which are sequences with 100% of identity. Alignment and taxonomic assignment were done with SINA v1.2.1152 using SILVA 138.1 database (Pruesse et al. 2012). SINA uses Lowest Common Ancestor method. We configurated a "Min identity" of 0.8 and a maximum number of search results of 1 per sequence results in "best match" type. Sequences with low alignment quality (< 90%) and sequences identified as mitochondria or chloroplasts were removed from the analysis. Original ZOTU tables were normalized by rarefying the reads of all samples to the minimum threshold of 2550 reads/

sample. Rarefactions were repeated 100 times to avoid the loss of less abundant ZOTUs (Edgar 2016).

For phytoplankton, water samples from the water column at the center of the ponds were collected, stored in 250 mL amber-colored glass bottles, and fixed with 3 mL of Lugol's solution. Each sample was sedimented in 100 mL Utermöhl chambers for counting and identification. Zooplankton invertebrates (rotifers, copepods, and branchiopods) were sampled using a hand net (63 μm mesh-size) through c. 10 m of water column whenever possible, integrating all different microhabitats. We fixed these samples using 4% formaldehyde (final concentration, v/v). Benthic invertebrate samples (mollusks and aquatic arthropods, among other groups) were collected using a hand net (20 × 20 cm, 250 μm mesh-size). About 10 m were sampled integrating all microhabitats. These samples were fixed with 96% ethanol. Samples of phytoplankton, microinvertebrates, and macroinvertebrates were identified to species level whenever possible, following methods and references as in Gálvez et al. (2023).

Finally, amphibian species occurrences were recorded in situ by identifying adults, larvae, eggs and calls. Due to their easy detectability and low species richness in Mediterranean ponds, they were surveyed using a hand net (800 cm^2, 2 mm mesh pore) with a constant effort of 10 min, and examining the pond surroundings for 10 more minutes. In tropical ponds, with higher species richness and lower detectability, we performed night surveys looking for individuals in the pond surroundings with an effective effort of up to 2 h per pond, avoiding full moon nights (Wilkinson 2015).

Diversity measures and statistical analyses

We explored alpha, beta and gamma diversities of different groups of organisms, comparing between tropical and Mediterranean ponds. The specific analyses described below were performed separately on each of the following groups of organisms: bacteria, archaea, phytoplankton, microinvertebrates (zooplankton and ostracods), macroinvertebrates (all collected benthic invertebrates except ostracods), and amphibians. Diverse and widespread groups which were not identified to genus level (i.e., Nematoda and Bdelloidea) were excluded from further analyses in order to avoid spurious drops in beta diversity estimations. However, other groups with low frequency of occurrence (< 5%; e.g., Bryozoa, Gordiacea, or Platyhelmintha) were included to avoid decreases at the three levels of diversity.

Using a spatial focus (Fig. 1), we measured different components of biological diversity for each group of organisms at each sampling period in both sets of ponds separately. Regarding gamma diversity, we calculated the extrapolated species richness (Chao index) of the species pool for each region and sampling period using the *specpool* function in the *vegan* R package (Oksanen et al. 2019). In order to check if sampling effort covered similar proportions of the total species pool, necessary to make data comparable, we explored the sample coverage per number of sampled units using the *iNEXT* function in *iNEXT* R package (Hsieh et al. 2016). Focusing on alpha diversity, we obtained the observed values for species richness (Hill numbers of order 0), transformed Shannon diversity (Hill numbers of order 1; Chao et al. 2013) and Simpson diversity (Hill numbers of order 2; Chao et al. 2014) in each pond. For this purpose, we used the *ChaoRichness*, *ChaoShannon*, and *ChaoSimpson* functions in the *iNEXT* R package. Shannon and Simpson diversities were not obtained for amphibians, due to the lack of abundance data for this group. We also estimated the classical evenness index of Pielou (J) as the ratio of the (untransformed) Shannon index to the logarithm of the number of species. We tested the relationship between gamma and alpha diversity using a standard major axis regression (Legendre and Legendre 1998), with the function *lmodel2* in the homonymous R package (Legendre 2018). For spatial beta diversity, we analyzed the dissimilarity of each pair of local communities of each region and each sampling period independently (Fig. 1), in order to avoid pairwise comparisons between ponds of different sampling periods, and discarding ponds without any species records. For this purpose, we used the Bray–Curtis dissimilarity index, by means of the function *beta.pair.abund* in the R package *betapart* (Baselga and Orme 2012). Amphibian beta diversity was calculated using the Sørensen index, due to the absence of abundance data. The comparison of the different components of biological diversity (except for gamma diversity) between regions and sampling periods was performed using Generalized Linear Mixed Models (GLMM; using Poisson distribution for species richness, quasi-Poisson distribution for Shannon and Simpson diversities, and quasi-binomial distribution for spatial beta diversity and evenness). We used the pond (or two ponds, in pairwise beta diversity data) as random variables to control for nonindependence in the data. We evaluated differences in environmental heterogeneity between regions and sampling periods using tests of homogeneity of multivariate dispersion (PERMDISP, Anderson 2006), by means of the *betadisper* function in *vegan*. We also tested for differences in total environmental heterogeneity, and separately in local physico-chemical variables (limnological heterogeneity) and climate variables (climate heterogeneity) with PERMDISP analyses. Differences in heterogeneity between regions and sampling periods were analyzed with ANOVA tests applied to the distances to the centroid obtained with the PERMDISP analyses.

Finally, using a temporal focus, and in order to compare the diversity variability in each site through time, we calculated the coefficient of variation of alpha diversity (species richness and transformed Shannon and Simpson indices) for each pond across the three sampling periods. In addition, we also estimated the dissimilarity between different sampling periods for each pond (i.e., temporal beta diversity). Temporal beta diversity was estimated with the Bray-Curtis (and Sørensen for amphibians) dissimilarity index, by means of the *beta.multi.abund* function in *betapart* R package. We only analyzed those ponds with species records for all the three sampling periods (23 ponds in the

tropical region, 29 ponds in the Mediterranean region), excluding ponds that were dry in one sampling campaign. Differences between regions in temporal beta diversity and in the coefficients of variation of alpha diversity were tested using GLMs (quasi-Poisson for coefficients of variation and quasi-binomial for temporal beta diversity). In order to assess the temporal

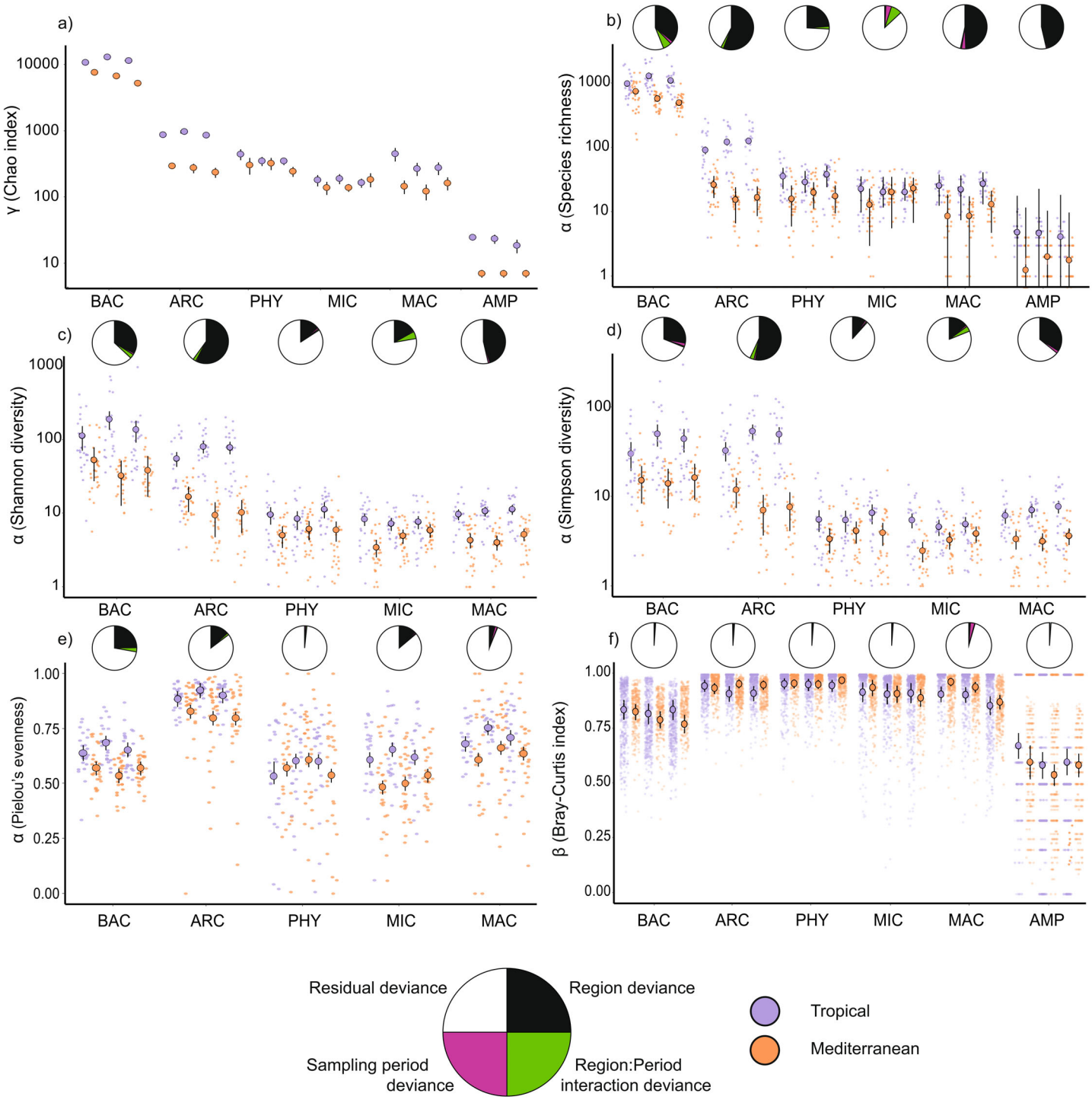

Fig. 3. Observed (small dots) and predicted (large dots) values by GLMMs with 95% confidence interval for gamma (**a**: Chao index), alpha (**b**: species richness; **c**: transformed Shannon diversity; **d**: Simpson diversity, **e**: Pielou's evenness) and total beta diversity (Bray-Curtis index, **f**). Deviances are shown as pie charts (Region = black, Sampling period = pink, Region : Season interaction = green, Residuals = white). Lilac points for tropical ponds and orange points for Mediterranean. BAC, bacteria; ARC, archaea; PHY, phytoplankton; MIC, microinvertebrates; MAC, macroinvertebrates; AMP, amphibians. Shannon and Simpson diversities, and Pielou's evenness, were not obtained for amphibians, due to the lack of abundance data for this group.

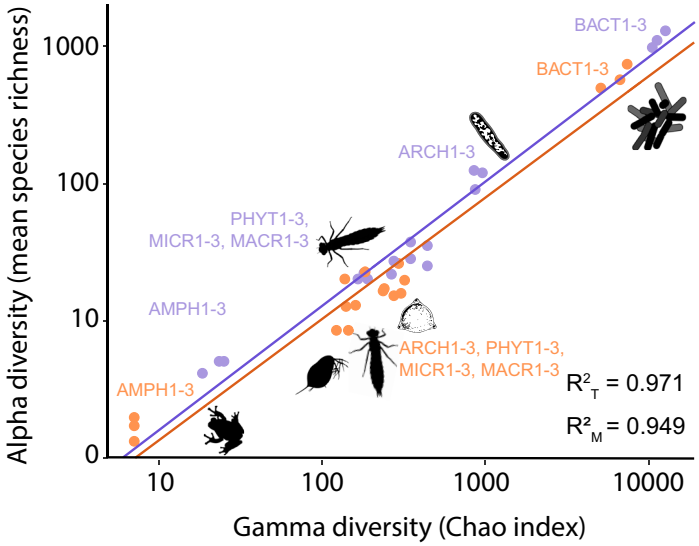

Fig. 4. Observed relationship between alpha diversity (as mean species richness) and gamma diversity (Chao index) for each sampling period (1, 2, or 3). R^2 for tropical (R^2_T; lilac) and Mediterranean (R^2_M; orange) regions in Standard Major Axis Regression are shown. BAC, bacteria; ARC, archaea; PHY, phytoplankton; MIC, microinvertebrates; MAC, macroinvertebrates; AMP, amphibians.

environmental heterogeneity, we calculated the distance to the centroid of each pond at different sampling periods, with a PERMDISP test. Distances to the centroid were used to test for differences in temporal environmental heterogeneity between regions with an ANOVA test. All analyses were performed with R 4.0.2 (R Core Team 2020).

Results

When analyzing diversity with a spatial focus, gamma diversity was generally higher in tropical than in Mediterranean ponds (Fig. 3a; Supporting Information Appendix 1, Table A1 for predicted values), and highly correlated with mean alpha diversity (Fig. 4). Sample coverage was similar in both sets of ponds and every group of organisms (Supporting Information Appendix 2, Fig. A1). However, gamma diversity of phytoplankton and microcrustaceans were very similar between regions at the middle or the end of the hydroperiod (Fig. 3).

Alpha diversity was significantly higher in the tropical than in the Mediterranean ponds in all groups, in terms of species richness and transformed Shannon and Simpson diversities, according to the GLMM analyses (Table 1; Fig. 3b–d; Supporting Information Appendix 1, Tables A1, A2 for predicted values and estimated parameters). We found significant differences in species richness between sampling periods (i.e., along the hydroperiod) in all groups of organisms except amphibians (Table 1). Richness of prokaryotic taxa in Mediterranean ponds declined after infilling, during the second sampling period, while Mediterranean eukaryotic richness was higher in the mid or late hydroperiod compared to the beginning. These significant seasonal differences, however, disappear in Shannon and Simpson diversities in all groups analyzed except for microinvertebrates. We also observed significant interactions between the sampling period and the regions, pointing to different trends in alpha diversity through time between regions (Table 1). However, regional differences were proportionally stronger than temporal effects (or than

Table 1. Parameter estimation in GLMMs predicting alpha (species richness) and spatial beta diversity (Bray-Curtis index except Sørensen for Amphibia) for each group of organisms.

Model	Random variables (variance)	Intercept	Region (tropical)	Sampling period 2	Sampling period 3	Region (tropical): Sampling period (2) interaction	Region (tropical): Sampling period (3) interaction
Species richness							
Bacteria	0.076	6.563*	0.284*	−0.259*	−0.409*	0.538*	0.521*
Archaea	0.259	3.176*	1.162*	−0.535*	−0.457*	0.820*	0.780*
Phytoplankton	0.221	2.602*	0.899*	0.230*	0.098	−0.440*	−0.032
Microinvertebrates	0.126	2.494*	0.551*	0.454*	0.573*	−0.565*	−0.686*
Macroinvertebrates	0.091	2.089*	1.106*	−0.004	0.409*	−0.124	−0.333*
Amphibia	0.036	0.277	1.341*	0.397	0.249	−0.414	0.455
Total spatial beta diversity							
Bacteria	<0.001	1.403*	0.0136	−0.209	−0.310*	0.092	0.302
Archaea	<0.001	2.235*	0.030	0.259	0.170	−0.611*	−0.509
Phytoplankton	<0.001	2.494*	−0.111	−0.032	0.222	−0.024	−0.332
Microinvertebrates	<0.001	2.272*	−0.298	−0.293	−0.439*	0.237	0.411
Macroinvertebrates	<0.001	2.587*	−0.694*	−0.282	−0.903*	0.266	0.525*
Amphibia	0.252	0.499*	0.171	−0.382*	−0.212	−0.007	−0.118

*p-value < 0.05. Reference levels for categorical variables are the Mediterranean region and the first sampling period.

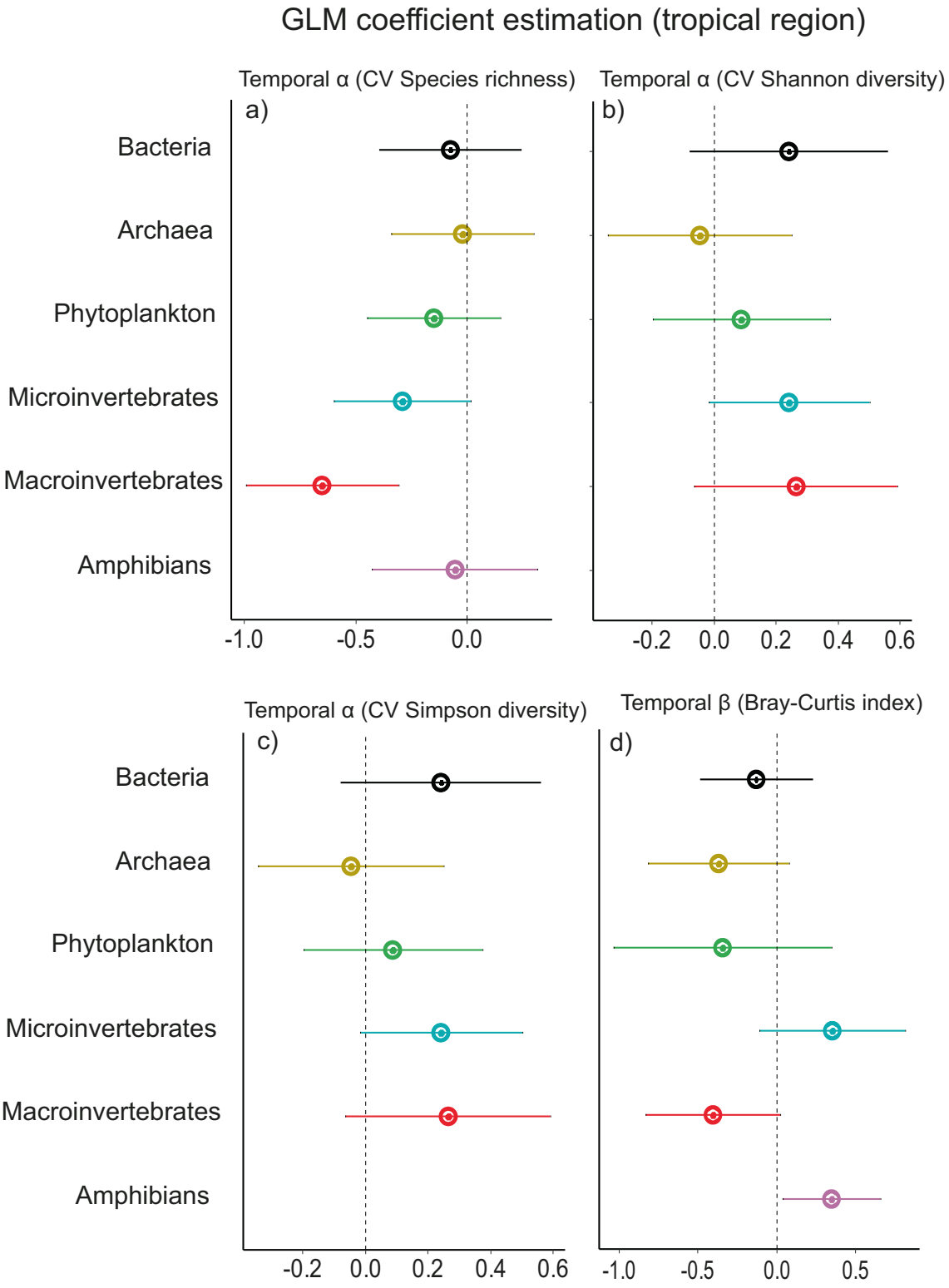

Fig. 5. Coefficient estimates and 95% confidence interval for tropical ponds in Generalized Linear Models of temporal alpha and beta variation: coefficient of variation of species richness (**a**), transformed Shannon diversity (**b**), Simpson diversity (**c**), Bray-Curtis index (**d**). Shannon and Simpson diversities were not obtained for amphibians, due to the lack of abundance data for this group.

interactions between region and sampling period), as shown by the large fractions of deviance explained by the regional variable (Fig. 3). Pielou's evenness was usually higher in tropical than in Mediterranean ponds (Appendix 1, Table A2).

In contrast to alpha diversity, spatial beta diversity did not differ between regions in most groups, except macroinvertebrates, which show significantly higher beta diversity in the Mediterranean region (Fig. 3f, Table 1; Supporting Information Appendix 1, Table A1 for predicted values). Temporal effects are variable but bacteria, microinvertebrates, macroinvertebrates, and amphibians showed a significantly lower beta diversity during the mid or late part of the hydroperiod compared to its initial part (Table 1). Nevertheless, the proportion of deviance explained by temporal or regional effects on beta diversity was highly variable and generally low or even null (Fig. 3f). We found no differences in PERMDISP tests in total environmental heterogeneity between each sampling period within the same region (but higher non-significant environmental heterogeneity in the first sampling period in both regions), and no differences were found between regions within the same sampling period. However, the studied Mediterranean ponds showed higher limnological heterogeneity at every sampling period, while tropical ponds showed higher climate heterogeneity (Supporting Information Appendix 1, Table A3).

Using a temporal approach, the coefficient of variation of alpha diversity barely differed between regions in terms of species richness, Shannon and Simpson diversities, according to the GLMs (Fig. 5a–c; Supporting Information Appendix 1, Tables A4, A5 for parameter estimation and predicted values). Only macroinvertebrates showed significantly higher temporal variation in species richness in Mediterranean than in tropical ponds. Regarding temporal beta diversity (Fig. 5d; Supporting Information Appendix 1, Tables A4, A5 for predicted values), GLMs do not show differences between regions except for amphibians, with higher values in the tropics. Temporal environmental heterogeneity was significantly higher in the Mediterranean ponds according to an ANOVA test ($p < 0.001$).

Discussion

In this study, we compared alpha, beta and gamma diversities of biological communities in two sets of temporary ponds located in two distant regions, Neotropical and Mediterranean, with marked climate and latitudinal differences. Overall, the tropical ponds harbored higher gamma diversity than Mediterranean ponds for most groups and sampling periods. Even though alpha diversity was also higher in the tropical set of ponds, spatial beta diversity was similar in both regions. Temporal variability in alpha and beta diversity was also found not to differ between regions, with the exception of a couple of groups of organisms.

Gamma and alpha diversity are higher in the tropics

As expected, the extrapolated regional species richness (gamma diversity) was generally higher in the tropical ponds, in agreement with the well described latitudinal diversity gradient (Rosenzweig 1995; Hillebrand 2004). Gamma diversity was highly correlated with alpha diversity, suggesting that a higher regional species pool in the tropics corresponded to higher local species richness, supporting previous findings (Arellano and Halffter 2003; García et al. 2007). Indeed, all three alpha diversity measures (i.e., order 0, 1, and 2) tended to be higher in tropical ponds in most groups.

Higher (transformed) Shannon and Simpson diversities in tropical ponds, apart from the effect of higher species richness, also reflected higher evenness in most groups, although the differences between regions were only significant in microinvertebrates and bacteria. In other words, species proportions in tropical ponds were more evenly distributed (not necessarily implying less rarity but maybe less dominance), a pattern also found in tropical spider communities by Privet and Petillon (2020). More intense and frequent biotic interactions in tropical ponds, such as predation, competition or facilitation, could determine the patterns observed (MacArthur 1972). For example, the absence, or low occurrence, of predators like fish in temporary ponds may allow large cladoceran species to survive and dominate the zooplankton of Mediterranean communities, displacing smaller and weaker competitors (Lemma et al. 2001) such as rotifers, which are usually the component of zooplankton with more species in these regions (Olmo et al. 2016), and consequently reducing microinvertebrate evenness.

Time did not generally drive substantial changes in alpha diversity (as shown by the low explained deviances in the GLMMs), but all groups except amphibians experienced a marked temporal variation in species richness. This variation was probably driven by increasing temperatures in the Mediterranean region (Rosset et al. 2010; Parain et al. 2019). Other variables that could be affecting the environmental conditions for various taxa later in the hydroperiod include macrophyte growth, increasing dissolved oxygen concentration, habitat heterogeneity and food availability (Battle and Godallay 2001). In contrast, alpha diversity of tropical ponds generally shows more reduced changes with time, or perhaps these changes are produced earlier in the hydroperiod and are therefore not detected in our temporal sampling scheme. Even though tropical ponds also experience a strong environmental seasonality due to hydrological changes because of seasonal heavy rains (Thomaz et al. 2007), this seasonality does not seem to be much reflected in the local communities of living organisms, at least in terms of alpha diversity, except in bacteria and archaea, with higher diversity as the hydroperiod advanced, perhaps facilitated by higher dispersal during the flooding season and by their fast population growth.

Spatial beta diversity does not differ between regions

We found no consistent differences for most groups in spatial beta diversity between the studied Mediterranean and tropical ponds. These results are in contrast with the latitudinal rule applied to beta diversity (see Soininen et al. 2018), at least for these freshwater ecosystems and at this spatial extent. Thus, differences in gamma diversity across these regions are mainly related to differences in alpha diversity, not beta diversity, in temporary ponds.

Environmental heterogeneity is considered a major mechanism generating differences in beta diversity (e.g., Melo et al. 2009), even reversing the latitudinal beta diversity gradient (Alahuhta et al. 2017). The absence of differences in beta diversity in these two sets of ponds, in contrast to the expected higher beta diversity in the tropical ponds, could be explained by no observed major differences in environmental heterogeneity between regions or by the higher limnological heterogeneity in the Mediterranean ponds.

However, the role of environmental heterogeneity can be masked by other processes (Heino et al. 2013). Connectivity may be an important explanation for these results. In a drier terrestrial matrix, Mediterranean ponds can harbor more isolated communities than tropical ponds, which are often more hydrologically connected or homogenized by seasonal strong precipitation events (Thomaz et al. 2007; Brasil et al. 2020). On the other hand, stronger dispersal barriers (Janzen 1967) or reduced species distributions (MacArthur 1972; Rapoport 1975) can lead to higher beta diversity in the tropical ponds. Thus, a combination of different homogenizing and heterogenizing processes could lead to similar beta diversities in both studied sets of ponds, at least in freshwater organisms.

Spatial beta diversity shows significant decline with time in most of the groups, with lower dissimilarities between ponds during the second or the third sampling periods. This decline is especially consistent in the tropical region, suggesting certain metacommunity homogenization, stronger in the tropical than in the Mediterranean ponds, during the rainy season (Thomaz et al. 2007). This is supported by the higher (but not significant) environmental heterogeneity during the first sampling period in both sets of ponds. However, deviances explained by this temporal variable are very low. Apart from abiotic environmental homogenization, we expect that the longer the time from the beginning of the hydroperiod, the higher the opportunities for dispersal-driven colonization and consequently increasing biotic homogenization of the metacommunity.

Temporal variation is not different across regions

Temporal variability in alpha and beta diversities at the pond level did not differ between both sets of ponds in most groups, suggesting that temporal changes in each local community are similar in the studied tropical and Mediterranean ponds. In other words, if there are purely temporal effects or time-dependent environmental effects driving changes in each local community, they are equally intense in both regions. Our results, therefore, do not support the findings by Liang et al. (2015) on higher species turnover at lower latitudes, but are rather in concert with the results of Nunes et al. (2020), who found no significant differences in temporal beta diversity in ant metacommunities at different altitudes (which could be considered analogous to latitudinal gradients). Therefore, differences in the temporal variability of diversity between ponds located in different regions are not clearly observed despite the higher seasonality in temperate regions (MacArthur 1972; Fick and Hijmans 2017; Olmo et al. 2022), which leads to higher temporal environmental heterogeneity found in the Mediterranean ponds.

Biological diversity across taxa

Some studied groups of organisms do not strictly follow the patterns described above, and deserve a mention apart. Among all the groups, only Mediterranean microinvertebrates matched or exceeded the local species richness observed in tropical ponds and, together with phytoplankton, also gamma diversity, particularly in the mid or late hydroperiod. This anomalous pattern has already been discussed for cladocerans (Dumont 1994), the most abundant branchiopod group. It is possible that the generally higher macroinvertebrate and amphibian species richness in tropical ponds, and the more recurring presence of fish, may cause a top–down effect, reducing the planktonic microcrustacean diversity in tropical ponds (Ferreira et al. 2018). Regarding temporal variation in alpha diversity, bacteria and archaea of Mediterranean ponds show a decreasing trend in alpha diversity across time with increasing temperatures through the hydroperiod, as also found by Parain et al. (2019). This may be related to competition effects, with some dominant species proliferating and displacing poor competitors (Zeng et al. 2019). Contrarily, both Mediterranean microinvertebrates and macroinvertebrates had higher alpha diversity in the late hydroperiod. Winter temperatures may be a harsh enough environmental condition to limit species hatching, dispersal and survival in temperate areas, underlying an increase in alpha diversity as air and water temperature rise (Rosset et al. 2010). Indeed, the sampling campaigns in our Mediterranean ponds survey started with low temperatures in winter and ended in the warmer late spring. The pattern was somehow inverted for tropical ponds, with increasing alpha diversity in prokaryotic organisms through the hydroperiod, and decreasing gamma diversity for invertebrates. Perhaps in this region the flooding events allowed rapidly growing bacteria and archaea to disperse and colonize wide areas without excluding competing species, but invertebrates may have suffered from growing populations of predators or dilution effects.

Spatial beta diversity was heterogeneous across groups of organisms, being lower in bacteria than in archea, algae or invertebrates, perhaps in relation to higher dispersal and

richness in the former, but with minor differences between regions. Higher beta diversity in Mediterranean invertebrates could be related with more isolation compared to the homogenized tropical communities (Brasil et al. 2020). Higher beta diversity in tropical bacteria, archaea and amphibia, although not significant, could be related to fast growth coupled to high dispersal rates preventing competitive exclusion in the former (Zeng et al. 2019) or to smaller geographic ranges in the later (Whitton et al. 2012). In addition, we found significant decreases of spatial beta diversity at the end of the hydroperiod in three groups, bacteria, microinvertebrates, and macroinvertebrates, and no significant increases. The strongest decrease was observed in macroinvertebrates; whose high dispersal ability (or efficiency; most are flying active dispersers) can lead to interseason dispersal processes that produce certain metacommunity homogenization in late phases of the hydroperiod (Williams et al. 2007).

Regarding local variability in biological diversity, variation in species richness was higher only in the macroinvertebrates of Mediterranean ponds, when comparing different organisms between regions. This points to larger fluctuations in species richness due to patch colonization in the mid and late hydroperiods (Williams et al. 2007). In contrast, local communities of smaller organisms are highly influenced by egg-bank hatching and historical processes (Castillo-Escrivà et al. 2017), or they may undergo fluctuations that cannot be detected at the studied temporal scale. Contrarily, dispersal limitation modulated by hydrological connectivity shifts and dispersal barriers must be less variable in the studied tropical system. Finally, only amphibians had significantly higher temporal beta diversity in the tropical ponds, suggesting faster succession or perhaps certain competitive exclusion for this group in the richest tropical region.

Conclusions

Our research design, with multiple taxa being surveyed over the same time period in different regions, with the same methodology and with similar sample coverages, has been successfully able to disentangle the relationship between the three components of diversity comparing two sets of ponds at distant latitudes. Consistent with the longstanding view in the literature, the gamma diversity of temporary ponds was higher at lower latitudes, but these differences were mainly related to differences in alpha diversity, not to spatial beta diversity, which did not differ between regions. In addition, spatial beta diversity was higher for various groups in the early hydroperiod in both regions, suggesting increasing homogenization through the ecological succession. Finally, both sets of ponds were similarly variable in terms of environmental and diversity heterogeneity through time. Thus, latitudinal differences in gamma diversity are not related to temporal but to spatial variation in diversity, specifically in alpha, not beta diversity.

Data availability statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.16586348.v3

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Conflict of Interest

None declared.

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